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RESEARCH ARTICLE

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Key Points:

- We present a mechanistic model resolving sedimentary organic carbon and infaunal macrobenthos
- Our model emphasizes variations of bioturbation both spatially and temporally depending on local food resources and macrobenthic biomass
- Our relatively simple implementation may further improve models of early diagenesis and marine food web dynamics

Supporting Information:

- Supporting Information S1

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Mutual Dependence Between Sedimentary Organic Carbon and Infaunal Macrobenthos Resolved by Mechanistic Modeling

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Abstract The mutual dependence between sedimentary total organic carbon (TOC) and infaunal macrobenthos is here quantified by a mechanistic model. The model describes (i) the vertical distribution of infaunal macrobenthic biomass resulting from a trade-off between nutritional benefit (quantity and quality of TOC) and the costs of burial (respiration) and mortality, and (ii) the variable vertical distribution of TOC being in turn shaped by bioturbation of local macrobenthos. In contrast to conventional approaches, our model emphasizes variations of bioturbation both spatially and temporally depending on local food resources and macrobenthic biomass. Our implementation of the dynamic interaction between TOC and infaunal macrobenthos is able to capture a temporal benthic response to both depositional and erosional environments and provides improved estimates of the material exchange flux at the sediment-water interface. Applications to literature data for the North Sea demonstrate the robustness and accuracy of the model and its potential as an analysis tool for the status of TOC and macrobenthos in marine sediments. Results indicate that the vertical distribution of infaunal biomass is shaped by both the quantity and the quality of OC, while the community structure is determined only by the quality of OC. Bioturbation intensity may differ by 1 order of magnitude over different seasons owing to variations in the OC input, resulting in a significant modulation on the distribution of OC. Our relatively simple implementation may further improve models of early diagenesis and marine food web dynamics by mechanistically connecting the vertical distribution of both TOC and macrobenthic biomass.

Plain Language Summary Processes for input, transport, and preservation of organic carbon (OC) in seabed surface sediments are pivotal in both regional and global carbon cycles. Among all involved processes, bioturbation by medium- to large-size (body size >0.5 mm) benthic animals is most important for transport of organic carbon in seabed sediments. A key factor controlling distribution of benthic animals is food (OC). Foraging of benthic animals in turn brings down food (OC) into deeper sediments. So far, no quantitative link between vertical distributions of benthic animals and organic carbon has been established. Our study thus aims at filling this knowledge gap by mechanistically linking the two factors together. Our approach is able to improve estimates of carbon fluxes between water column and seabed and especially applicable for dynamic environments with sharp spatial and/or temporal gradients of environmental change.

1. Introduction

Early diagenesis of organic carbon (OC) in marine sediments plays an important role in both regional and global carbon cycles (e.g., Henrichs, 1992). Among a large number of influencing processes, three have been widely recognized as pivotal for early diagenesis of OC in marine sediments: input, transport, and preservation (e.g., Berner, 1980; Blair & Aller, 2012; Boudreau, 1997; Hedges & Keil, 1995; Rodil et al., 2008; Schwartzkopf, 1993; Wijsman et al., 2002). Input of OC to the seabed is mainly controlled by pelagic factors such as current shear stress, near-bed concentration of OC, and pelagic primary production, while transport and preservation of OC are driven to a large extent by processes within the seabed. Bioturbation has been recognized as the most important process for OC transport in sediments (e.g., Meysman et al., 2006; Jørgensen & Parkes, 2010); however, it exists only within a certain range (normally up to ~40 cm) beneath the sediment-water interface as constrained by the oxygen demand of bioturbating animals (e.g., Jørgensen & Parkes, 2010; Kristensen et al., 2012). Preservation of OC in marine sediments is largely determined by a competition between the burial (i.e., sedimentation) rate and the degradation rate (Burdige, 2007). Although degradation of OC occurs both aerobically and anaerobically (Middelburg et al., 1993), its rate is greatly enhanced by oxygen (Kristensen et al., 1995), which is quickly depleted within the uppermost

centimeters of sediment. Given that the uppermost tens of centimeters of marine sediments host the most dynamic processes of input, transport and preservation of OC, an understanding of a benthic-pelagic coupling in this thin transitional zone is crucial for studying not only the carbon cycles (e.g., Soetaert et al., 2000) but also marine ecosystems and their functioning (e.g., Marcus & Boero, 1998; Navarrete et al., 2005).

Models for early diagenesis of OC in marine sediments have been developed for more than three decades since the pioneering work by Berner (1980). State-of-the-art diagenetic models resolve a complex network of biogeochemical reaction pathways along a one-dimensional sediment column (e.g., Berg et al., 2003; Dhakar & Burdige, 1996; Jourabchi et al., 2005; Katsev et al., 2004; Morse & Eldridge, 2007; Soetaert et al., 1996; Soetaert & Middelburg, 2009; Wijsman et al., 2002). The fate of sedimentary OC is normally modeled through an advection-diffusion-reaction type of equation that is built on the principle of mass conservation. Most diagenetic models include the effect of bioturbation in a simplified; thus, either constant or only depth-dependent way, but bioturbation, induced by the movement of local infauna, is expected to vary spatially and temporally depending on the community structure and biomass of infaunal macrobenthos in situ (Rosenberg, 2001). Such model simplification reflects the difficulty in a quantification of bioturbation rates by direct observation in situ (Queirós et al., 2013). The bioturbation rates are, at best, fitted using observed vertical distributions of radioactive tracers, with derived values varying over 3 orders of magnitudes (10^{-2} – 10 $\text{cm}^2 \text{d}^{-1}$) for different environments (e.g., Jørgensen & Parkes, 2010; Teal et al., 2008). A major problem arising from a fitting to observation of a limited number of field samples is that the spatial and temporal variability of bioturbation is largely ignored. This may induce significant errors when applying diagenetic models to areas characterized by sharp spatial and/or temporal gradients of abundance, community composition, and activity of benthic animals (e.g., Pennington et al., 2006; Rosenberg, 2001).

A key factor controlling the biomass and structure of the benthic macrofaunal community appears to be food availability (i.e., quantity of OC) (e.g., Gooday & Turley, 1990; Grebmeier et al., 1988; Heip et al., 1992; Pearson & Rosenberg, 1978, 1987; Rosenberg, 1995, 2001). However, little attention had been paid on the role of nutritional quality in shaping the structure of benthic macrofaunal community until the work by Dauwe et al. (1998). Since then, numerous studies have confirmed a comparable importance of food quality in regulating the biomass and structure of benthic macrofaunal community (e.g., Herman et al., 1999; Kröncke, 2006; Reiss & Kröncke, 2005; Rodil et al., 2008; Venturini et al., 2011; Wieking & Kröncke, 2003, 2005). So far, only a few modeling attempts have been made to reveal a quantitative link between infaunal macrobenthos and sedimentary OC (e.g., Kelly-Gerreyn et al., 2014; Whearcroft et al., 1990), yet none has explicitly taken into account the impact of food quality, which is found to impose a critical control on macrobenthic community structure in shallow-water environments such as coastal waters and shelf seas (Lopez & Levinton, 1987). Unraveling such link would enable us to predict the variation of the biomass and community structure of infaunal macrobenthos in response to a change of food supply in terms of quantity and quality in any given environmental setting. Development of such model would have to imply a more precise quantification of food quality for macrobenthos and to take into account the high variability in environmental settings relevant to macrobenthos such as degree of eutrophication, pollution, and gradient in hydrodynamic stress. Finally, and perhaps most importantly, given that OC supply is a major constraint for macrobenthos on the one side, and macrobenthos a major driver of transport and preservation of OC on the other side, the feedback arising from the interaction between OC and macrobenthos needs to become a new focal point of research.

Our study thus aims at quantifying the two-way relationship between infaunal macrobenthos (community structure and biomass distribution) and food (OC) in marine sediments. We present a mechanistic model linking the biomass and bioturbation diffusivity of infaunal macrobenthos with OC profiles and test it with published data for the North Sea. We specifically seek to improve existing early diagenetic models by dynamically connecting the vertical distribution of OC, bioturbation diffusivity, and macrobenthic biomass in a mechanistically sound way.

2. Materials and Methods

2.1. Characteristics of the Study Sites

The theoretical basis of our model is built on the results of Dauwe et al. (1998) who investigated the community structure and vertical distribution of biomass of macrobenthos in sediments at four selected sites in the

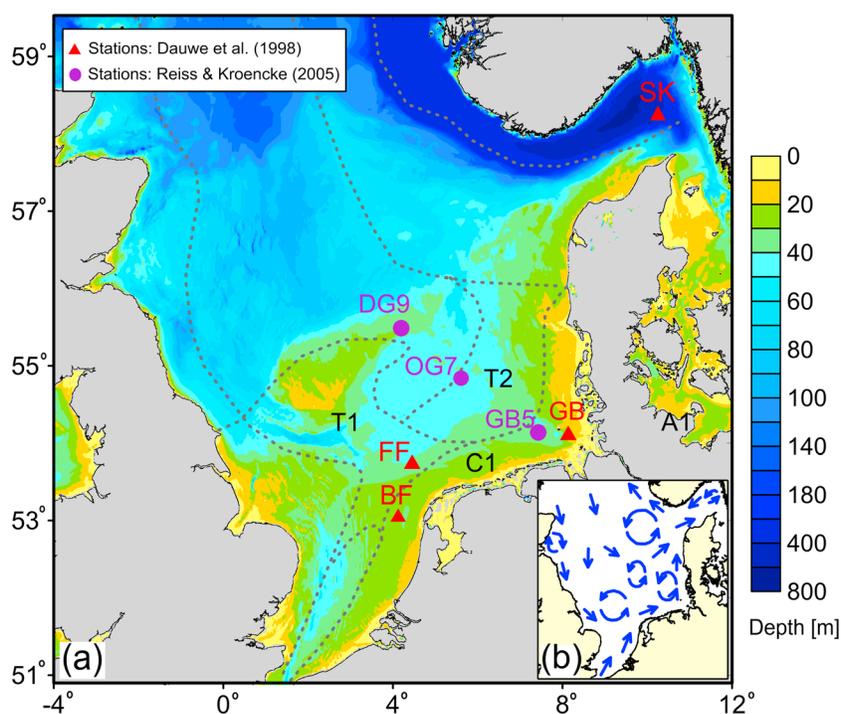


Figure 1. (a) Map of the North Sea with locations of the sampling stations in two studies (Dauwe et al., 1998; Reiss & Kröncke, 2005) used for model calibration and validation. A general classification of the water masses in the North Sea by Lee (1980) is also shown as dashed lines. Three water masses relevant to this study are as follows: The continental coastal water (C1) along the southeast coast and two zones (T1 and T2) which act as a transition between coastal and offshore waters. (b) The residual circulation pattern under weak wind conditions (modified from Nihoul (1980)) related to transport and deposition of OC.

North Sea (Figure 1). These sites were chosen to represent contrasting quantity and quality of OC and different hydrodynamic stresses. OC quality in sediments was categorized into three general classes, namely, fresh, intermediate, and refractory distinguished by the Chlorophyll *a* to TOC ratio. Dauwe et al. (1998) then found a clear dependence of the vertical distribution of macrobenthos on not only the quantity but also the quality of OC by intercomparison of the four sites. The German Bight sampling station (indicated by GB in Figure 1), characterized by a high sedimentation rate ($0.3\text{--}0.6\text{ cm a}^{-1}$) with surface sediments containing mostly fresh OC, was dominated by surface-feeding benthos (making 66% of total biomass in sediments). Total biomass (measured in ash-free dry weight, AFDW hereafter) of macrobenthos was also high at this site (38 g m^{-2}). The Skagerrak sampling station (SK in Figure 1) represents also a depositional environment with a mean sedimentation rate of 0.35 cm a^{-1} ; however, in contrast to the GB station, the OC deposited at this site was mostly refractory, because of (1) a relatively large water depth ($\sim 300\text{ m}$) and (2) a long distance to the major primary production area (i.e., the source area of fresh OC) along the south-eastern coast of the North Sea. Interface and suspension feeders were nearly absent here ($<2\%$ in terms of biomass) and sediments were inhabited mainly by small-sized deep-living deposit feeders (73% in terms of biomass). Biomass of macrobenthos at this site was on a medium level (12 g m^{-2}). The Frisian Front sampling station (FF in Figure 1), which is located in the transition zone between different water masses and characterized by a moderate sedimentation rate (0.1 cm a^{-1} on average) of intermediate quality of OC, hosted the highest diversity of trophic groups with largest individual size and deepest distribution among all stations. Biomass of macrobenthos at this site was also on a medium level (14 g m^{-2}). The Broad Fourteen sampling station (BF in Figure 1) represents a nondepositional nearshore sandy area. Despite of its location in the major primary production area, a constantly high hydrodynamic stress induced by strong currents and waves prohibits sedimentation of fine particles (Stanev et al., 2009). The lack of food supply greatly limited the abundance of macrobenthos at this site (0.2 g m^{-2}), being 2 orders of magnitude smaller than at other stations.

By a thorough analysis of these four sites, Dauwe et al. (1998) concluded that (1) the quality of input OC determines the community structure of macrobenthos, which further controls the bioturbation intensity, (2) the

bioturbation intensity in turn affects the vertical diffusion of OC, and (3) the vertical distribution of biomass of macrobenthos is a trade-off between the benefit (i.e., quantity and quality of food) and the cost (i.e., respiration and mortality). These qualitative descriptions form the basis for the construction of our numerical model presented next.

2.2. Model Description

A one-dimensional mass balance of TOC in marine sediments can be described an advection-diffusion-reaction equation:

$$\frac{\partial C}{\partial t} = -\frac{\partial wC}{\partial z} + \frac{\partial}{\partial z} \left(K_v \frac{\partial C}{\partial z} \right) + S, \quad (1)$$

where C is the volumetric concentration (mg g^{-1}) of OC, t is the time (days), z is the depth (cm) with $z = 0$ at the sediment-water interface and positive downward, w is the advection rate (cm d^{-1}) induced by sedimentation and compaction, K_v is the vertical diffusivity ($\text{cm}^2 \text{d}^{-1}$), and S is the source/sink term ($\text{mg g}^{-1} \text{d}^{-1}$). Lateral transport of C is neglected in the equation due to its subordinate impact compared to vertical transport (Berner, 1980).

Although TOC in sediments is composed of dissolved and solid parts, its profile mainly reflects the distribution of solid OC given that the mass concentration of solid OC is at least 3 orders of magnitude higher than that of dissolved OC (Ogawa & Tanoue, 2003). Based on this understanding our model simulates solid OC only and regards its profile identical to the TOC profile that is normally obtained from lab measurement. Following the work of Dauwe et al. (1998) and the concept of multi-G models (Berner, 1980; Jørgensen, 1978), solid OC is classified into three different pools in the model: labile (i.e., of high-quality nutrient), semilabile (i.e., of intermediate quality nutrient), and refractory (i.e., of low-quality nutrient). The mass balance equation of each pool (with $i = 1$ for labile, $i = 2$ for semilabile, and $i = 3$ for refractory) is given by

$$(1-p) \frac{\partial C_i}{\partial t} = -\frac{\partial w(1-p)C_i}{\partial z} + \frac{\partial}{\partial z} \left(K_v(1-p) \frac{\partial C_i}{\partial z} \right) - (1-p) \left(R_i + (1-\varepsilon_i) \gamma \frac{B}{\rho_s} \right) C_i, \quad (2)$$

where p is sediment porosity which is assumed to exhibit an exponential decay ($e^{-k_1 z}$) until a certain depth, and the last term on the right-hand side represents the net loss due to degradation and macrobenthic uptake (digestion). R_i is the first-order degradation (i.e., remineralization) rate constant of Pool i ($i = 1, 2, \text{ and } 3$) and is also assumed to decay exponentially ($e^{-k_2 z}$) along depth, $B(z, t)$ is the time-dependent biomass density of macrobenthos (g m^{-3}) at depth z , ρ_s is the sediment density (g m^{-3}), γ is the macrobenthic uptake coefficient representing the ratio of the amount of sediment particles processed by macrobenthos to the biomass of macrobenthos per unit time (day). Lopez and Levinton (1987) found that deposit feeders daily processed at least the same amount of sediment as their own body weight, thus $\gamma \geq 1$. $\varepsilon_i (\leq 1)$ is the portion of ingested OC that is not digested by macrobenthos. For modeling simplicity $(1-\varepsilon_i)\gamma$ is represented by a single parameter γ_i^* .

The temporal change of biomass of macrobenthos $B(z, t)$ at depth z is described by

$$\frac{\partial B}{\partial t} = (G - L)B, \quad (3)$$

where G and L represent the rate of gain (e.g., recruitment and production) and loss (e.g., respiration cost and mortality) at depth z , respectively.

$G(z)$ is assumed to be exclusively dependent on available food resources that are distinguished into two types: (1) food resources within the sediment column that are reachable by benthos through vertical movement (bioturbation) and (2) local food resources located within a small range around depth z that requires minimum moving effort. We assume that the two types of food resources jointly determine $G(z)$:

$$G(z) = \sum_{i=1}^3 a_i C_i(z) \left(\int_{z'=0}^{z_1} a_i C_i(z') dz' - \Delta z a_i C_i(z) \right) z_1^{-1}, \quad (4)$$

where the coefficient a_i ($i = 1, 2, 3$) represents the efficiency of the OC pool i in terms of gaining macrobenthic biomass, with higher-quality OC gaining biomass more efficiently as expressed by $a_1 > a_2 > a_3$. The impact of food quality on macrobenthos is explicitly distinguished by these three coefficients. z_1 is the reachable depth

limit for macrobenthos. $z_1 = 30$ cm is applied in our model according to simulation results showing a negligible difference in a variation of z_1 between 30 and 50 cm. In case of high-spatial resolution in discretization of the sediment column (i.e., Δz is small enough), equation (4) can be simplified by

$$G(z) = \sum_{i=1}^3 a_i^2 C_i(z) z_1^{-1} \int_{z'=0}^{z_1} C_i(z') dz'. \quad (5)$$

The argument for the above formulation is that an increase of macrobenthic biomass at depth z is affected by not only the average food resource within the reach limit, which shall have a uniform effect on macrobenthic biomass at all depths, but also the food resource located exactly at z , which shall have a maximum effect on benthos located at the same depth.

The gain of macrobenthic biomass is directly associated with the amount of uptake. The efficiency of macrobenthic uptake in gaining biomass also depends on both the quantity and quality of ingested OC. For modeling simplicity a linear relationship is assumed:

$$\alpha \sum_{i=1}^3 \gamma_i^* \frac{B_i C_i}{\rho_s} = \sum_{i=1}^3 a_i^2 C_i B_i z_1^{-1} \int_{z'=0}^{z_1} C_i(z') dz', \quad (6)$$

where α represents the ratio of the gain of macrobenthic biomass to the uptake. B_i and C_i can be canceled out on both sides, resulting in

$$\sum_{i=1}^3 \gamma_i^* = \rho_s z_1^{-1} \alpha^{-1} \sum_{i=1}^3 a_i^2 \int_{z'=0}^{z_1} C_i(z') dz'. \quad (7)$$

Equation (7) indicates a dependence of uptake rate (γ_i^*) on available food resources, especially the amount of high-quality food. To be consistent with the efficiency in gaining macrobenthic biomass, a proportional relationship $\gamma_1^*/a_1 = \gamma_2^*/a_2 = \gamma_3^*/a_3$ is used to derive γ_i^* ($i = 1, 2, \text{ and } 3$). Although the gain of biomass includes production and recruitment, we assume that the amount of uptake is still larger than the gain of biomass, that is, $\alpha < 1$. Sensitivity of model results to a variation of α is analyzed and described in following sections.

$L(z)$ comprises two terms: cost for respiration and mortality, and is described by

$$L = L_1 e^{k_1 z} B + L_2 e^{-k_1 z} B, \quad (8)$$

where $L_1 e^{k_1 z} B$ represents the cost for respiration. L_1 is an environmental-dependent coefficient influenced by various factors such as temperature, oxygen level, and sediment properties. For modeling simplicity its value is derived empirically by model calibration. The term $e^{k_1 z}$ reflects an increasingly higher cost for respiration (e.g., due to deficiency of oxygen and sediment consolidation) of moving (mixing) down the sediment column, which is consistent with the exponential decay of sediment porosity (p). Mortality is assumed to be controlled mainly by predation and dependent upon biomass (Kelly-Gerreyn et al., 2014). Predation-induced mortality is assumed to be highest at sediment-water interface and exhibits an exponential decay along depth due to respiration cost (thus the same k is used in the exponential function). L_2 is another empirical coefficient to be derived by model calibration.

A steady (equilibrium) status of the biomass implies that the net gain (G) equals the net loss (L), leading to

$$B(z) = e^{-k_1 z} \sum_{i=1}^3 a_i^* C_i(z) \int_{z'=0}^{z_1} C_i(z') dz', \quad (9)$$

where $a_i^* = a_i^2 (L_1 + e^{-2k_1 z} L_2)^{-1} z_1^{-1}$ ($i = 1, 2, \text{ and } 3$).

Bioturbation diffusivity $K_v(z, t)$ plays a central role in linking the diagenetic and ecological model parts. Realistically, it is a complex function of body size, abundance, and vertical foraging intensity of infaunal macrobenthos. Since body size and abundance of infaunal macrobenthos jointly scale with biomass through a power law (e.g., Duplisea, 2000; Kelly-Gerreyn et al., 2014), and foraging intensity is directly linked to the nutritional need for metabolism and growth, for modeling simplicity $K_v(z, t)$ is assumed to scale with the local macrobenthic biomass $B(z, t)$ through a power law and inversely proportional to the value of local food resource:

$$K_v = \beta B^b \left(\sum_{i=1}^3 a_i C_i \right)^{-1}, \quad (10)$$

where β is a prefactor to be quantified through model calibration with observational data, b is a scaling coefficient linking body size and abundance to biomass. A constant value $b = 1.33$ is used according to Kelly-Gerreyn et al. (2014) who confirmed that biomass in shelf sediments broadly scales with body size through a quarter power law (Brown et al., 2004) and abundance through a $-3/8$ power law (Schmidt-Nielsen, 1984).

The biophysical meaning for the above formulation of K_v is that the bioturbation diffusivity at depth z is assumed to be dependent upon (1) the body size and abundance of infaunal macrobenthos (through scaling with biomass) located at z and (2) the effort macrobenthos need to make (i.e., vertical movement) to derive enough nutrition for their metabolism and growth. The latter depends on the local food resource ($\sum_{i=1}^3 a_i C_i$), that is, intensified vertical movements when local food resource becomes less. Through a link to local macrobenthic biomass and food resource, both of which may vary temporally and spatially, the dynamic aspect of K_v is explicitly emphasized in our formulation.

To distinguish the dominance of macrobenthic community structure between surface-feeding (e.g., suspension, interface, and surface deposit feeders) and deep-feeding (subsurface and deep-living feeders) mode, a depth parameter z_0 which divides the total infaunal biomass into two equal portions is introduced:

$$\int_{z=0}^{z_0} B dz = \int_{z=z_0}^{z_1} B dz. \quad (11)$$

A small value of z_0 indicates that macrobenthos are concentrated near the sediment-water interface, while an increase of z_0 suggests that macrobenthos tend to distribute more evenly along depth. The value of z_0 can thus be used as a proxy for the community structure in terms of biomass.

Numerical solution of the model is performed on a one-dimensional grid with a temporal variable index of z to ensure that $z = 0$ always applies to the sediment-water interface. Sediment deposition and erosion are both taken into account. For details of the numerical scheme the reader is referred to the supporting information.

3. Results: Model Application and Analysis

3.1. Model Calibration and Validation

Middelburg et al. (1993) pointed out that the division of OC pools in multi-G models and their corresponding degradation rates should be determined through fitting. The derived partitioning of (measured) TOC into distinct OC pools should be regarded as model fit parameters specific to the observational data set. On the other hand, degradation of OC differs between aerobic and anaerobic setting, with a higher rate at seafloor surface (i.e., freshly deposited) and a decreased rate along with a burial into deeper sediments (e.g., Burdige, 2007; Hedges & Keil, 1995; Kristensen et al., 1995; Middelburg et al., 1993). Based on this understanding and Figure 4 of Middelburg et al. (1993) which indicates that the range of OC degradation rate in marine environment lies between 10^{-8} and 10^{-1} d^{-1} in the 90% confidence interval, the first-order degradation rate constant (R_i , $i = 1, 2$, and 3) for each OC pool on seafloor surface ($z = 0$) is parameterized (Table 1). Setting of these values is based on existing literature, for example, $R_1(z=0) = 5.5 \times 10^{-2} \text{ d}^{-1}$ applies to fresh phytoplanktonic material which contains a significant fraction of labile compounds such as chlorins, fatty acids, and amino acids that are of high nutrition for benthos (Westrich & Bemer, 1984) and $R_3(0) = 5.5 \times 10^{-5} \text{ d}^{-1}$ is valid for refractory material which is of low nutritional quality (Dauwe et al., 1998). $R_2(0) = 5.5 \times 10^{-3} \text{ d}^{-1}$ is introduced in our model for intermediate quality material (e.g., detritus) which may originate from dead phytoplankton and has undergone limited cycles of deposition/resuspension. Dependence of R_i on burial depth is implemented by $R_i(z) = e^{-k_2 z} R_i(0)$, where k_2 is an empirical coefficient to be derived by model calibration. With prescribed degradation rates, the partitioning of (measured) TOC into the three OC pools at each study site is based on Dauwe et al. (1998) (described previously) and further fine tuned through a model fitting to observational data. Technical details of the calibration procedure and optimization of model parameters (i.e., a_i ($i = 1, 2$, and 3), L_1 , L_2 , k_1 , k_2 , and β) are provided in the supporting information.

Table 1
Parameter Setting in the Model

Parameter	Unit	Value	Source
$R_1(0)$	d^{-1}	5.5×10^{-2}	(1)
$R_2(0)$	d^{-1}	5.5×10^{-3}	(3)
$R_3(0)$	d^{-1}	5.5×10^{-5}	(2)
w_{GB}	$cm d^{-1}$	1.6×10^{-3}	(2)
w_{SK}	$cm d^{-1}$	1×10^{-3}	(2)
w_{FF}	$cm d^{-1}$	0.3×10^{-3}	(2)
w_{BF}	$cm d^{-1}$	1×10^{-5}	(2)
α	/	0.5	(3)

Note. Sources: (1) Westrich and Bemer (1984); (2) Dauwe et al. (1998); and (3) parameter defined in this study.

The resultant calculated curves of TOC and macrobenthic biomass distribution for all four stations are illustrated in Figure 2, with corresponding parameters listed in Table 2. Root-mean-square error (RMSE) normalized by the mean value of the measured data is calculated to evaluate the model performance. The simulated TOC profiles ideally fit the measured values at three stations (BF, FF, and SK) with normalized RMSE less than 0.1. Larger errors in the modeled TOC profile, with normalized RMSE = 0.29, occur at station GB where the measured TOC content exhibits a drastic variation between 4 and 10 cm depth. Such abrupt change is not reproduced in our model result. The simulated biomass profiles are in good agreement with the measured ones, with normalized RMSE less than 0.1 at three stations (BF, GB, and SK) and 0.26 at station FF, where the measured biomass is almost equally distributed at depths above 10 cm. The overall degradation rate ($R = f_1 R_1 + f_2 R_2 + f_3 R_3$, where f_i

is the fraction of Pool i in TOC) derived from model calibration for each station (Table 2) also shows good agreement with the information of Dauwe et al. (1998) that is briefly described in section 2.1.

All calibrated parameters, except for L_1 and L_2 , are constant among all four stations. The three yield coefficients a_i ($i = 1, 2$, and 3), representing the efficiency of the OC pools in gaining macrobenthic biomass, indicate a relationship $a_1 = 2.7a_2 = 17a_3$. This constant relationship suggests that the impact of food quality on benthos is spatially uniform. A constant value for k_1 (= 0.11) suggests a mild exponentially increased cost for respiration of mixing down the sediment column. The constant value for k_2 (= 0.3) indicates an enhanced decay of OC degradation rate compared to porosity. The derived value for β (= 0.22) indicates a constant scaling of bioturbation diffusivity with macrobenthic biomass and local food resource. In contrast to the above mentioned parameters, the calibrated values of L_1 and L_2 differ significantly among stations, suggesting their site dependency. The largest and smallest value of L_1 occurs at GB and BF, respectively, differing by more than 70 times. It is worth to note that the best fit values of L_1 and L_2 at BF are exceptionally small compared to those at other stations (Table 2). This is attributed to two reasons: (1) In contrast to other stations, BF is in nondepositional or erosional status (Dauwe et al., 1998) which is not resolved in our model calibration based on a constant and positive sedimentation rate (Table 1); and (2) since L_1 represents the impact of respiration cost, its spatial variability among the stations, especially between GB and BF, might be attributed to oxygen supply since Dauwe et al. (1998) indicated anoxic condition below a surface fluffy sediment layer (a few cm) at GB while a large oxygen penetration depth (>5 cm) at BF. Value of the mortality-related coefficient L_2 is of the same order of magnitude as L_1 at all stations, suggesting that both mortality and respiration cost are important in constraining macrobenthic biomass at the sediment-water interface. A clear dominance of L_1 , which is nearly twice of the value of L_2 , is shown at GB, confirming a major impact of respiration cost at this muddy site (mud content >80%). By contrast, although SK contains also a large amount of mud (mud content >90%) and TOC, surface macrobenthic biomass here is not predominantly controlled by respiration cost, since L_2 is only slightly less than L_1 . At the other two sites BF and FF L_2 is larger than L_1 , suggesting that mortality is more important in constraining surface macrobenthic biomass at these sandy sites (mud content <40%). It is especially worthy of note that below the sediment-water interface mortality decreases rapidly (e.g., dropping to half of its surface value at $z = 3$ cm according to model result), while on the other hand, respiration cost increases and becomes a major constraint for macrobenthic biomass in deeper sediments.

The calibrated bioturbation diffusivities K_v are plotted in Figure 3a for the four stations. Dauwe et al. (1998) also provided a dimensionless estimate of K_v at these stations (Figure 3b) based on a simple formulation proposed by Whearcroft et al. (1990) that correlates bioturbation diffusivity with individual size and total number of macrobenthos in situ. A comparison between our model result and estimate by Dauwe et al. (1998) indicate that they are in general consistent. The major difference is in the uppermost 5 cm at SK, where K_v is much reduced in the estimation of Dauwe et al. (1998) compared to our calculation. According to our model result, the value of K_v at the sediment-water interface ranges from 0.05 to 0.57 $cm^2 d^{-1}$, with minimum at BF and maximum at GB. This range agrees with the study of Teal et al. (2008), in which the mean value of K_v in the North Sea was found to be 0.16 $cm^2 d^{-1}$, with a standard deviation of 0.24 $cm^2 d^{-1}$. It is worth to note that although K_v has its largest surface value at GB, it

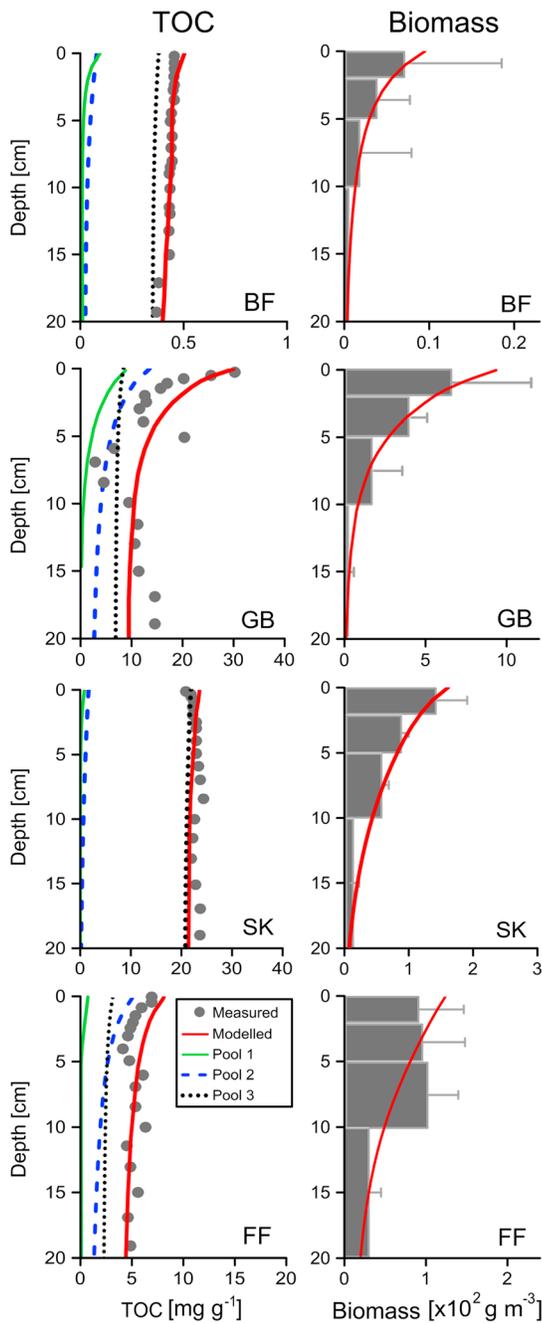


Figure 2. Vertical distribution of measured TOC and macrobenthic biomass (mean \pm standard error) at four stations (see locations in Figure 1) in Dauwe et al. (1998) and corresponding results by our model. Note that the biomass is measured by ash-free dry weight.

decreases fastest along depth among all four stations. Furthermore, the calculated value of z_0 (as indicator for the community structure) at this site (= 3 cm) is smallest among all four stations. A combination of such information indicates that macrobenthos at GB are dominated by surface-feeding animals which move (forage) intensively at and near the sediment-water interface. In contrast to other stations which exhibit an exponential decay of K_v along depth, K_v at FF remains relatively stable ($\approx 0.22 \text{ cm}^2 \text{ d}^{-1}$) in the uppermost 5 cm and then declines with a much milder slope along depth. Below $z = 10 \text{ cm}$ K_v is largest at FF among all stations (Figure 3). The corresponding value of z_0 is 4.6 cm at FF. A combination of such information indicates that macrobenthos at FF tend to distribute evenly along depth and their vertical movements are very active. The largest value of z_0 (5 cm) appears at both stations BF and SK, suggesting a predominant role of deep-living feeders in the community structure that is confirmed by Dauwe et al. (1998).

3.2. Sensitivity Analysis

Sensitivity tests, in which the model parameters are tuned, are carried out to quantify and rank the importance of several environmental factors in determining the distribution of OC and macrobenthos in sediments. Results will also help to simplify the model formulation and input.

3.2.1. Sensitivity to Macrobenthic Uptake

The importance of the net OC loss due to uptake by macrobenthos is evaluated. Two constant ratios of the gain of macrobenthic biomass to the uptake, $\alpha = 1$ and 0.05, are tested, respectively. A comparison of the net loss caused by macrobenthic uptake with that due to first-order degradation (R_i , $i = 1, 2$, and 3) in each OC pool is shown in Figure 4. In the result of $\alpha = 1$ (Figure 4a), the uptake rate by macrobenthos is subordinate compared to the first-order degradation rate R_1 for Pool 1 (i.e., labile OC) at these stations, with exceptions only below 20 cm at GB and FF where both quantities are of the same order of magnitude. For Pool 2 (i.e., semi-labile OC), the uptake rate is also of subordinate importance compared to R_2 in upper part (10 cm) of sediments at most stations, with the only exception at GB, where a large density of biomass ($\sim 1,000 \text{ g m}^{-3}$) is hosted. For Pool 3 (i.e., refractory OC), the uptake rate by macrobenthos is consistently larger than R_3 at three stations (FF, SK, and GB). These two quantities are comparable only in case of a low density of macrobenthos (e.g., BF). In the result based on $\alpha = 0.05$, that is, the uptake rate by macrobenthos is increased by 20 times compared to the earlier one, the impact of macrobenthos on the OC pools becomes prominent (Figure 4b). Although being still of subordinate importance compared to first-order degradation for loss of Pool 1 in upper part (10 cm) of sediments at three stations (BF, FF, and SK), macrobenthic uptake is overwhelming compared to first-order degradation at GB. This result suggests that macrobenthos could significantly process (uptake and vertically transport) fresh OC where they exist in a high density (more than several hundred g m^{-3}), which is in good agreement with the isotope tracer study by Kamp and Witte (2005) in the German Bight revealing a rapid subduction and uptake of fresh phytodetritus by macrobenthos. Existing literature suggests that macrobenthic assimilation efficiency (the ratio of metazoan production to uptake) normally ranges in between 0.1 and 0.5 (e.g., Kelly-Gerreyn et al., 2014; Sturdivant et al., 2013). We assume that the additional impact by recruitment is not larger than production; thus, the results of our sensitivity tests should represent the lowest and highest possible impact of macrobenthic uptake on a net loss of OC, respectively. Based on such outcome a mean value of $\alpha = 0.5$ is used.

Table 2
Model Parameters Derived Through Calibration With Field Data

Parameter	Unit	SK	GB	BF	FF
a_1	d^{-1}	0.67	0.67	0.67	0.67
a_2	d^{-1}	0.25	0.25	0.25	0.25
a_3	d^{-1}	0.04	0.04	0.04	0.04
k_1	/	0.11	0.11	0.11	0.11
k_2	/	0.3	0.3	0.3	0.3
β	$m^5 g^{-1} d^{-2}$	0.22	0.22	0.22	0.22
L_1	$m^3 g^{-1} d^{-1}$	0.7	1.3	0.017	0.21
L_2	$m^3 g^{-1} d^{-1}$	0.5	0.75	0.02	0.64
R	d^{-1}	6.4×10^{-5}	8.8×10^{-3}	2.5×10^{-4}	3×10^{-3}

In summary, the relative importance of local macrobenthic uptake in a net loss of TOC compared to first-order degradation is (1) comparable at sites dominated by labile OC that foster a large density of biomass (more than several hundred $g\ m^{-3}$), (2) comparable at sites dominated by semilabile OC that foster a medium density of biomass ($\sim 100\ g\ m^{-3}$), and (3) dominant at sites dominated by refractory OC.

3.2.2. Sensitivity to Bioturbation Diffusivity

The major difference between our model and conventional diagenetic models is that we correlate the distribution of TOC with local infaunal macrobenthos through the bioturbation diffusivity K_v that varies both spatially and temporally. To evaluate the impact of the variability of K_v on the vertical distribution of OC and biomass, we

designed three scenarios with different parameterizations of K_v (Table 3) and compare their results with the reference result based on equation (10). Scenario S1_ K_v is based on the mean values derived from model calibration. The mean vertical curve of K_v at the four stations can be satisfactorily approximated by an exponential function described in Table 3 with normalized RMSE = 0.01. Scenario S2_ K_v is based on the mean value from Teal et al. (2008) described previously and also adopts an exponential decay along depth. In contrast to other scenarios which assume an exponential decay of K_v , Scenario S3_ K_v adopts a constant value along depth. Setting of other parameters in these scenarios follows the reference simulations presented previously.

The reference model results with a dynamic K_v display the best overall performance (with a mean normalized RMSE = 0.14 for TOC and 0.12 for biomass profiles, respectively, for all four stations) on approximating both TOC and biomass distribution (Figure 5). Among different parameterizations of K_v , a constant value along depth (i.e., Scenario S3_ K_v) yields the largest errors, which are especially obvious for the TOC profiles at BF (normalized RMSE = 0.15) and SK (normalized RMSE = 0.12). This parameterization overestimates the TOC content with an increasing bias along depth. Compared to a constant K_v along depth, simulations adopting an exponential decay of K_v produce better fits to measured data. Scenario S1_ K_v based on the mean values derived from model fitting has a better overall performance (with a mean normalized RMSE = 0.16 for TOC and 0.18 for biomass profiles, respectively) than Scenario S2_ K_v based on the mean value from Teal et al. (2008) (with a mean normalized RMSE = 0.17 for TOC and 0.21 for biomass profiles, respectively). It is worth to note that the bioturbation diffusion plays a critical role in transporting OC, especially the labile and

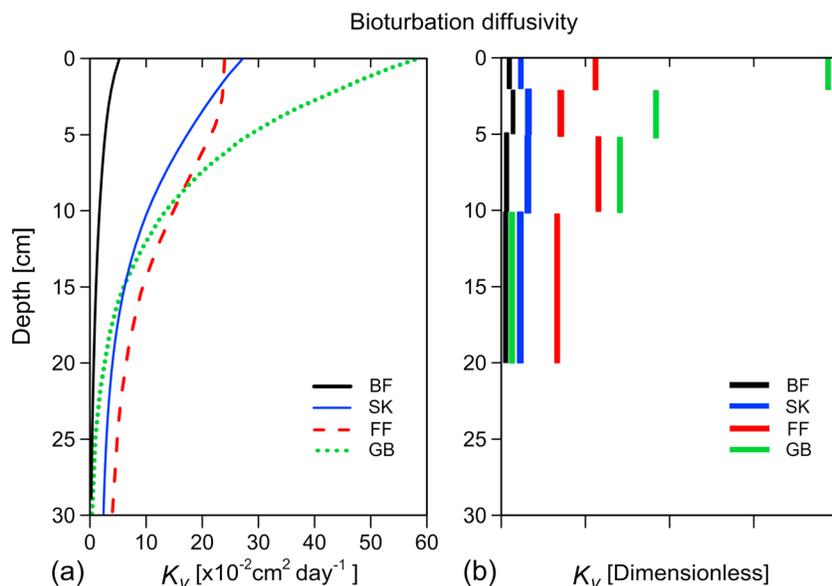


Figure 3. (a) Model-derived bioturbation diffusivity for the four North Sea stations. (b) Dimensionless relative bioturbation diffusivity estimated in Dauwe et al. (1998). Note that the field data cover only the uppermost 20 cm and averaged in four depth strata (0–2, 2–5, 5–10, and 10–20 cm).

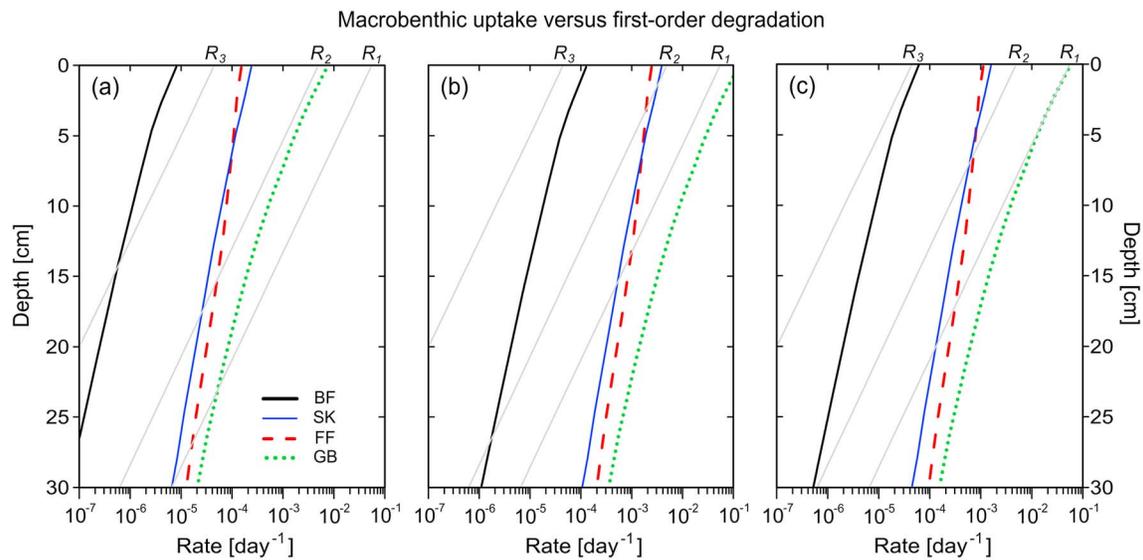


Figure 4. Vertical distribution of the uptake rate by macrobenthos (slash lines) at the four stations based on (a) $\alpha = 1$, (b) $\alpha = 0.05$, (c) and $\alpha = 0.5$, respectively, compared to the profiles of first-order degradation rate of three OC pools (indicated by solid lines in grey).

semilabile components, into deeper part of the seabed. A model run excluding this term (i.e., $K_v = 0$ for all depths) results in a rapid decrease of the TOC content as well as biomass along depth, which are significantly biased from the measured data.

In summary, a dynamic K_v dependent upon local macrobenthos and food resources produces results closest to observations. In case of absence of observational data for vertical distribution of TOC and macrobenthos in sediments, an exponential decay of K_v along depth is able to provide reasonable estimates. Vertical profiles of macrobenthos and TOC at a specific site are moderately sensitive to a certain oscillation ($\pm 40\%$) of K_v around a mean value estimated from field samples collected in the area.

3.2.3. Sensitivity to Sedimentation Rate

Sedimentation rate w , for a given site, is kept constant in most diagenetic models, including our previous model runs. However, sedimentation rate and the associated input of OC are highly variable in natural environment. To assess the impact of this temporal variability on the vertical distribution of TOC and biomass, we introduce a variable w in the model runs. Two scenarios (Table 3) are designed for this purpose. Scenario S1_w assumes a half-year oscillation of w between $0.5w_{ref}$ (representative for autumn and winter condition) and $1.5w_{ref}$ (for spring and summer), where w_{ref} represents the reference sedimentation rate at station FF given in Table 1. An amplified oscillation between $-w_{ref}$ and $3w_{ref}$ is implemented in Scenario S2_w. Negative value of w represents seabed erosional rate. In both scenarios the net annual sedimentation rate is equal to w_{ref} . For simplicity, the boundary input and output rate of each OC pool is assumed to be dependent upon the sedimentation rate and thus is also modified in accordance with w , that is, increased by the same amplitude as sedimentation rate does in case of deposition,

and set to zero in case of erosion. The reference profiles at FF (Figure 2) serve as the initial condition for the simulations.

Clearly, a seasonal variation in the sedimentation rate significantly affects the fate of TOC and macrobenthos (Figure 6). Profiles of both TOC and biomass of macrobenthos oscillate accordingly. The amplitude and penetration depth of this oscillation increases with increasing variation in w . In spring and summer, when sedimentation rate and input flux of OC are high, the biomass of macrobenthos is concentrated in the uppermost few centimeters (Figure 6c) where fresh food is located. The corresponding bioturbation diffusivity in surface sediments is high. However, the value of z_0 decreases along with an increase in sedimentation rate, suggesting that surface-feeding fauna dominates the community structure. In

Table 3
Scenarios Designed for the Sensitivity Analysis

Scenarios	Parameter setting
S1 _{K_v}	$K_v = 0.25e^{-0.066z} \text{ cm}^2 \text{ d}^{-1}$
S2 _{K_v}	$K_v = 0.16e^{-0.066z} \text{ cm}^2 \text{ d}^{-1}$
S3 _{K_v}	$K_v = 0.16 \text{ cm}^2 \text{ d}^{-1}$
S1 _w	$w = \begin{cases} 1.5w_{ref}, & \text{for spring and summer} \\ 0.5w_{ref}, & \text{for autumn and winter} \end{cases}$
S2 _w	$w = \begin{cases} 3w_{ref}, & \text{for spring and summer} \\ -w_{ref}, & \text{for autumn and winter} \end{cases}$

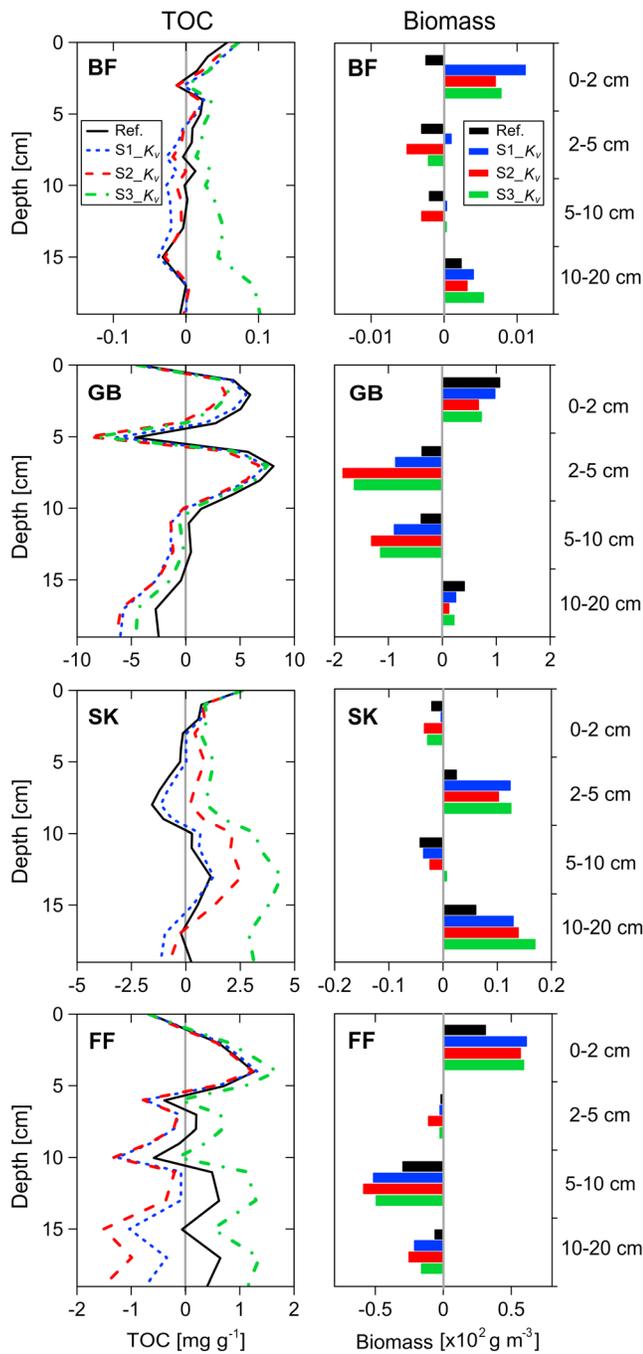


Figure 5. Difference between the modeled and measured data (result = modeled value – measured value) for four model simulations in which K_v is tuned. Note that the modeled biomass is vertically averaged in four depth strata (0–2, 2–5, 5–10, and 10–20 cm) to be consistent with the measured data.

model results of these scenarios with the field data is able to provide information of the composition of OC pools, their temporal variation as well as the response of macrobenthos.

It is straightforward to understand that the modeled biomass based on the labile (i.e., Pool 1) and the refractory (i.e., Pool 3) OC represent the upper and lower limits of model-predicted biomass of macrobenthos, respectively. All field data (measured means), except for that of September 2000 at GB5, fall into the modeled range (Figure 7). GB5 displays the highest TOC concentration (2–3.8 mg g^{-1} , mean = 3.2 mg g^{-1}) and

autumn and winter, when deposition at the seabed is greatly reduced or the seabed is in an erosional status, the lack of OC input and degradation of existing OC result in a reduction of both food quantity and quality. As a consequence, the value of z_0 is large and the community structure is characterized by deep-feeding deposit feeders. Biomass and bioturbation diffusivity in the food-starved season are significantly reduced compared to the situation in spring and summer. In Scenario S2_w characterized by alternation between deposition and erosion, bioturbation diffusivity differs by 1 order of magnitude over different seasons.

Seabed erosion greatly modifies the profiles of both TOC and macrobenthos in sediments. In contrast to depositional circumstances in which the maximum of both TOC content and macrobenthic biomass is located at the sediment-water interface, erosion of the seabed surface results in a downward shift of the maximum of both quantities (Figure 6). The subsurface location of the maximum induced by erosion may explain the observed distribution of macrobenthic biomass at FF (Figure 2), which was not ideally reproduced by a constant and positive w .

In summary, the vertical distribution of TOC and macrobenthos turn out to be highly sensitive to a variation in the sedimentation rate of OC. This high sensitivity imposes challenges for modeling dynamic environments characterized by sharp spatial and/or temporal gradients in sedimentation.

3.3. Modeling Temporal Macrobenthic Variability

For an examination of the model ability to capture temporal variability in benthic geoecological states, independent data sets from another three sites (GB5, OG7, and DG9, see Figure 1) in the North Sea presented by Reiss and Kröncke (2005) are used. These data contain 16 monthly sampling cruises at these stations from September 2000 to May 2002. The biomass and TOC of each sample were measured in a total sum instead of vertical profiles. In the absence of vertical distribution in the original data, our model is used as a diagnostic tool to derive further insights into the relationship between TOC and macrobenthos.

The simulation is based on the means of the parameters derived from the calibration (Table 2) for consistency. To initiate the simulation, the time series of boundary conditions have to be specified. However, it is not possible to reliably define the input value of each individual OC pool due to lack of relevant information in the original data. Three scenarios, in which the TOC is assumed to be composed of one single OC pool, are therefore designed to specify the boundary input. Simulations are based on the measured means of TOC (Figure 7). Scenario S1 represents the labile OC pool, S2 stands for the semilabile OC pool, and S3 is for the refractory OC pool. A comparison of the

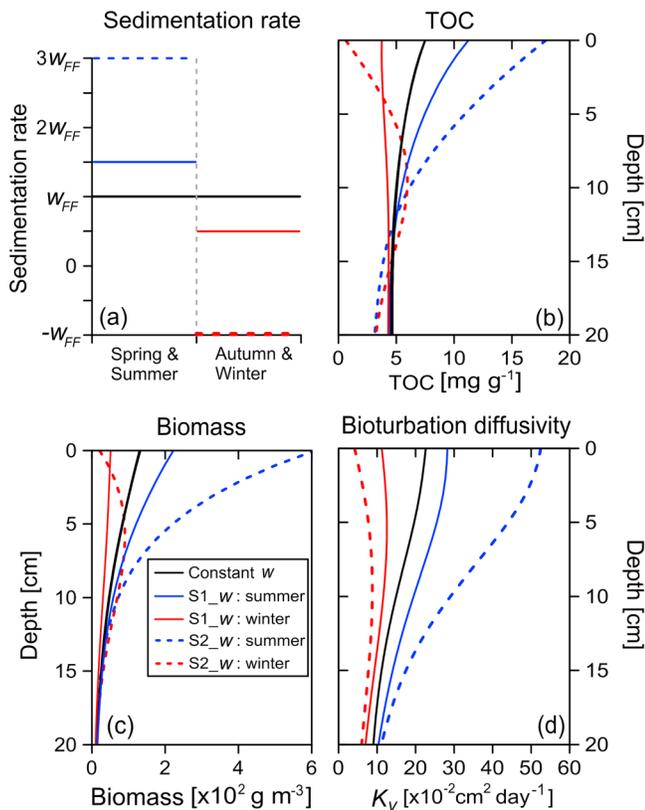


Figure 6. Simulation results of the two scenarios with a variable sedimentation rate w (associated with OC input) at the station FF and their comparison with the reference profiles based on a constant w . (a) The oscillation of w in the scenarios is shown. (c–d) Simulation results are shown, respectively.

biomass ($5.7\text{--}12.5\text{ g m}^{-2}$, mean = 8 g m^{-2}) among the three stations (Figure 7, left), and a comparison of the modeled biomass of each scenario with the field data at this station indicates that in a considerably long period (February–November 2001) the field data are smaller than the model results of Scenario S2 (Figure 7, right). Only in 3 months (September 2000, October 2000, and January 2002) the field data (biomass) are larger than the model results of Scenario S2, and in 7 months the field data are comparable to the model results of Scenario S2. This result suggests that the TOC at GB5 is mainly composed of semilabile and refractory components. As indicated by the data at stations FF and SK, a dominance of intermediate-to-refractory OC would result in a benthic community structure dominated by deep-living deposit feeders. This also applies to GB5 and justified by Reiss and Kröncke (2005) showing that the community structure in terms of biomass remained relatively stable at GB5 and was dominated by subsurface deposit feeders.

Measurements at OG7 show that both TOC ($1.3\text{--}2.9\text{ mg g}^{-1}$, mean = 1.9 mg g^{-1}) and biomass ($0.98\text{--}5.2\text{ g m}^{-2}$, mean = 3.2 g m^{-2}) at this station are on an intermediate level among the three stations. Most of the field data (biomass) quantitatively match the model results of Scenario S2, with a notable deviation only in 5 months. This may be interpreted as an indication that TOC at OG7 is mainly composed of semilabile component. As exemplified by the station FF, the predominance of the semilabile OC pool would result in a high diversity of trophic groups with largest individual size and deepest distribution. This pattern is indeed evidenced by the field data (Figure 6 in Reiss and Kröncke (2005)) showing comparable fractions taken up by subsurface deposit feeders, predators, and interface feeders in the total biomass at OG7. The measured Chlorophyll a to

TOC ratios at OG7 are in general larger than those at GB5. The slight increase in the food quality inferred from the increased Chlorophyll a to TOC ratios provides further support to our model results showing that the TOC at OG7 is of a larger degradation rate than that at GB5.

In contrast to GB5 and OG7, the most offshore station DG9 hosts the smallest content in both TOC ($0.57\text{--}0.96\text{ mg g}^{-1}$, mean = 0.7 mg g^{-1}) and biomass ($0.56\text{--}2.12\text{ g m}^{-2}$, mean = 1.4 g m^{-2}) but also displays the largest Chlorophyll a to TOC ratios, which imply an increase in the food quality. A good agreement with this signal is shown in our model results, showing that in most periods the field data (biomass) are larger than the model results of Scenario S2, with exceptions in only 3 months. Similar to station GB, dominance of fresh-to-intermediate OC would result in a dominance of organisms located near and at the sediment-water interface. This is also proved by the field data showing that DG9 is dominated by suspension and interface feeders as well as predators (Reiss & Kröncke, 2005).

According to our model results, an increase of food quality from refractory to fresh triggers a change of the community structure from deep-feeding to surface-feeding dominance, vice versa. Our model results also indicate several major changes in the food quality at each station. For example, the periods November 2001 to January 2002 (at GB5), September–November 2000 (at OG7), and May–Jun 2001 (at DG9) are characterized by a significant increase of food quality from intermediate refractory or intermediate to fresh, and the periods September–November 2000 (at GB5), January–April 2002 (at GB5), November 2000 to Feb 2001 (at OG7), and June–July 2001 (at DG9) are characterized by a significant decline of food quality. The increase in the former periods would imply a significant increase of the surface-feeding fauna, while the decrease in the latter would imply the opposite pattern. Overall, the field data (Figure 6 in Reiss and Kröncke (2005)) confirms a high validity of our model for most periods except for two (September–November 2000 and November 2001 to Jan 2002 at GB5).

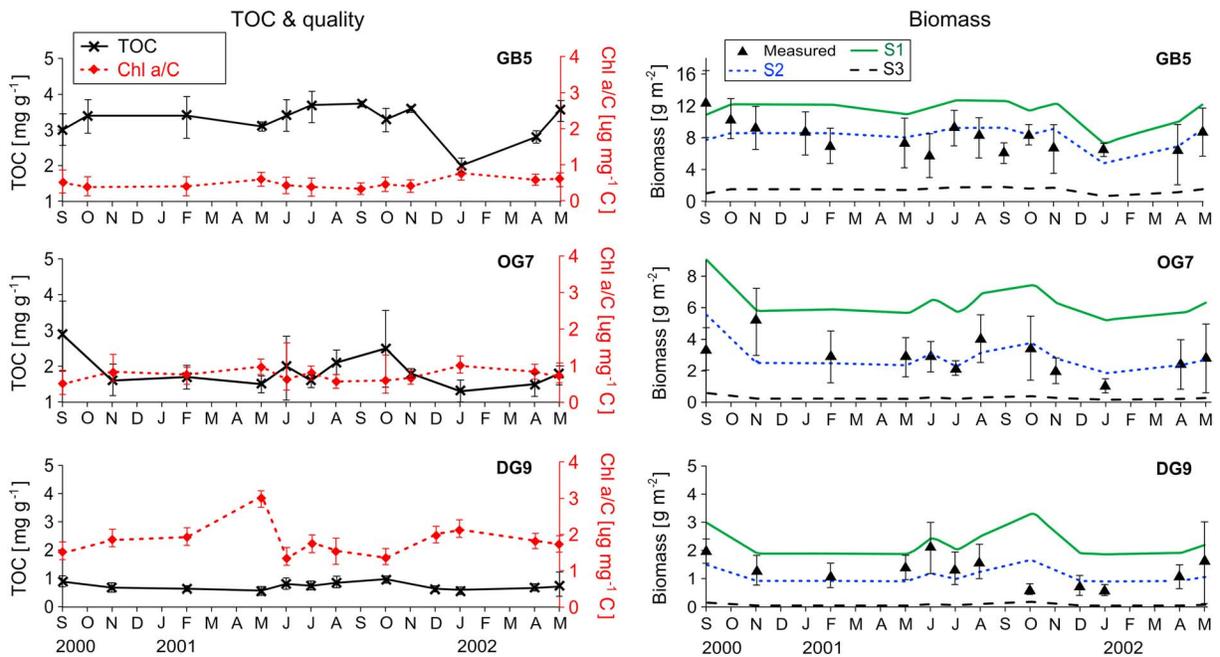


Figure 7. (left) Time series of TOC concentration and Chlorophyll *a* to TOC ratio at three stations GB5, OG7, and DG9 from measurement (mean ± standard error, from Reiss and Kröncke (2005)). (right) Time series of measured biomass (mean ± standard error) and model results of three scenarios (solid and dashed lines) at the stations. Note that model results are based on the mean values of measured TOC.

3.4. Macrobenthic Biomass and Community Structure: Dependence on TOC

The good agreement with field data provides us confidence to use the model for analyzing the correlation between sedimentary TOC and macrobenthos. A full spectrum of macrobenthic responses in terms of community structure and biomass is calculated by a continuous variation in the input of quantity and quality of TOC. Average values of L_1 and L_2 from the three depositional sites (FF, GB, and SK) are used in this calculation. Result in Figure 8a indicates a positive correlation between biomass and both TOC concentration and quality. The two factors equally determine the macrobenthic biomass as imprinted by equation (9). By

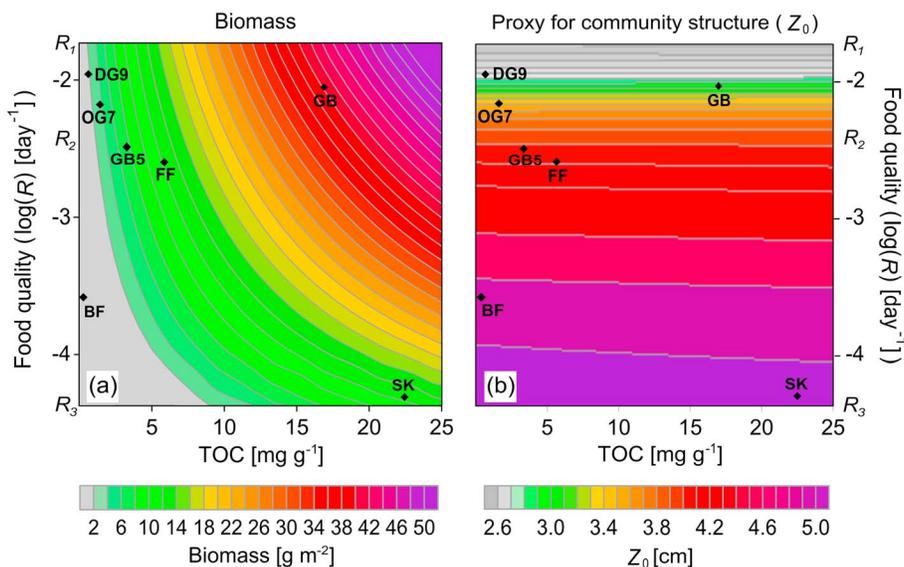


Figure 8. (a) Simulated biomass in relation to the quantity and quality of sedimentary TOC within the calibrated range. (b) Calculated value of z_0 (as proxy for macrobenthic community structure) in relation to the quantity and quality of TOC. Characteristics of the seven stations used in this study are indicated. Note that due to a use of averaged values of L_1 and L_2 , biomass is slightly overestimated at GB and underestimated at FF.

contrast, macrobenthic community structure, as reflected by the value of z_0 , depends only on the quality of the TOC (Figure 8b). It is particularly worthy of note that a large gradient in z_0 arises when the overall degradation rate R falls between 6×10^{-3} and $1.1 \times 10^{-2} \text{ day}^{-1}$. This range of degradation rate actually represents a food quality that is between fresh and intermediate according to our parameter setting (Table 1) and corresponds to the reconstructed rate at five stations, namely, DG9, GB, OG7, FF, and GB5. The community structure at these stations shifts from surface-feeding dominance (DG9 and GB) to deep-feeding dominance (FF and GB5) along with an increase of z_0 from 2.6 to 4.6 cm. This result indicates that z_0 can be used as a proxy for the community structure of macrobenthos. A small value of z_0 (≤ 3 cm) suggests dominance by surface feeders, while a large z_0 (≥ 4 cm) would imply dominance by deep-living feeders in the community structure. The transition of the community structure occurs within a relatively narrow range of z_0 where the TOC quality shifts between fresh and intermediate level.

4. Discussion

4.1. TOC as an Environmental Proxy

A conventional view on benthic ecology is that the structure and biomass of the faunal community are constrained by a variety of environmental factors, which comprise not only food supply but also temperature, salinity, oxygen, hydrodynamic shear stress, and sediment properties (e.g., grain size and mud content). However, implementing every involved factor as a variable in a mechanistic benthic modeling approach would make it a mission impossible. Principle of model reduction, which considers only the major driving factors as variable terms and integrate the ensemble impact of other subordinate factors as an average term, needs to be followed. Based on existing knowledge which reveals a primary control of food on benthos (see section 1 and references therein), we have constructed a mechanistic model linking these two objects. Good agreement with field data demonstrates that both infaunal community structure and biomass of macrobenthos can be satisfactorily predicted based on the quantity and quality of food (TOC), while the impact of some other environmental factors can be averaged into two site-dependent parameters, that is, L_1 and L_2 in equation (8). On the other hand, it is difficult to decouple food supply from the overall environmental setting, since quantity and quality of OC input to the seabed are highly correlated with other environmental factors such as hydrodynamic shear stress, temperature, and sediment properties. For instance, deposition of OC normally requires a weak hydrodynamic shear stress. Since organic detritus is normally integrated into flocs in natural waters, its deposition is often accompanied with settling of mud. Thus, the TOC content usually positively correlates with the mud content. The quality of TOC is related to the water depth as well as the distance to (coastal) areas with high primary production. Pelagic primary production varies seasonally due to changing sun light, temperature, and nutrient levels. Thus, the impact of various environmental factors is either implicitly described by the quantity and quality of food input to the seabed or explicitly implemented by model parameters (e.g., L_1 and L_2) which reflect the basal constraints. The variation in two parameters, L_1 and L_2 , among the four calibration stations (Table 2) emphasizes the importance of model calibration using local field data before its boarder application.

4.2. Model Applicability and Limitation

Pearson and Rosenberg (1978) proposed a graphic model for a general response of marine benthic communities to variations of organic carbon enrichment. When OC concentration is relatively low, biomass of macrobenthos increases along with an increase of OC. However, the increase of biomass starts to slowdown when OC reaches a threshold due to enhanced oxygen depletion and buildup of toxic by-products (ammonia and sulfide) associated with the degradation of OC. As OC further increases, these factors become gradually dominant in controlling the variation of biomass and at a second threshold lead to a negative correlation between OC content and biomass. In order to derive a quantitative understanding of these two critical thresholds, Hyland et al. (2005) analyzed the field data from 951 stations representing 7 coastal regions of the world including the North Sea and found that the two thresholds to be around 10 and 35 mg g^{-1} , respectively. However, it is worth to note that neither the original P - R curve nor the modified version by Hyland et al. (2005) takes into account explicitly the impact of the freshness (degradation rate) of OC on modulating the benthic response. High-quality OC, such as fresh phytoplanktonic detritus, has a higher degradation rate than low-quality OC. Thus, the thresholds for fresh OC should be different from those for refractory OC. Based on the findings by Dauwe et al. (1998) and others (see section 1) it is expected that a variation in the quality of OC

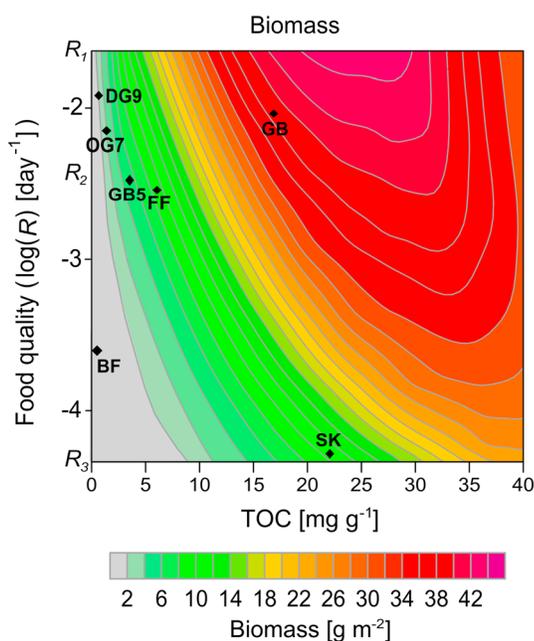


Figure 9. Extended spectrum of modeled macrobenthic biomass in relation to TOC enrichment taking into account detrimental effect caused by hypoxic conditions and production of toxins.

input would have a significant impact on the benthic response. Simulation results of our model demonstrate the complexity of the response of biomass to a variation in quality and quantity of OC, and to our knowledge, this study also presents the first modeling attempt to vertically resolve the mutual dependence between macrobenthos and sedimentary OC in a mechanistic manner.

Our model is calibrated using field data from the North Sea. The TOC concentrations (vertical means of the uppermost 20 cm of seafloor surface sediments) used for model calibration and validation range between 0.45 and 22 mg g⁻¹ (Figures 2 and 8). Outcome of the North Sea Observation and Assessment of Habitats (NOAH) project (<http://www.noah-project.de/habitatatlas/>) indicates that the TOC concentration in seafloor surface sediments rarely exceeds 14 mg g⁻¹ in the southern North Sea except at the nucleus of a few mud depocenters where mud content exceeds 80%. The TOC concentration at station GB (vertical mean of 17 mg g⁻¹, and maximum 30 mg g⁻¹ at surface), which is located at the nucleus of a mud depocenter off the Elbe river mouth with mud content exceeding 88% in its surface sediments, can thus be regarded as the upper limit of TOC content for the southern North Sea. Also, TOC concentrations at SK located at the major sink of fine-grained material of the region, that is, the Norwegian trench, with a vertical mean of 22 mg g⁻¹ and maximum of 25 mg g⁻¹ can be regarded as the upper limit. However, at both stations the TOC concentration is still below the critical threshold (~30–35 mg g⁻¹)

for a sign shift in the macrobenthic response. Thus, it can be stated that at least a major part of the North Sea represents a region where biomass of benthic macrofauna positively correlates with food (TOC) quantity and quality.

The major limitation of our model is the missing benthic response to excessive TOC enrichment (i.e., the second threshold). This hinders its application to seafloors with high TOC concentrations, such as estuaries and basins affected by hypoxia (Levin et al., 2009). A possible solution to this would be to relate the respiration term L_1 in equation (8) to the detrimental effect of TOC enrichment in terms of hypoxic conditions and production of toxins. For precise modeling, field data for settings with high TOC concentrations are needed to better define L_1 . Nevertheless, we could still investigate the feasibility of such solution based on limited field data support. For numerical simplicity, we assume a linear relationship between L_1 (cost for respiration) and the overall degradation rate R for TOC content exceeding 17 mg g⁻¹ (i.e., the value at GB). The relationship is derived based on the values at SK and GB which represents the lower and upper limits of calibrated R , respectively (Figure 8). This yields $L_1 = 90R + 0.5$. Adopting this relationship and assuming 30 mg g⁻¹ (labile OC) as the threshold for decline of macrobenthic biomass (Hyland et al., 2005), our model is able to produce an extended spectrum of macrobenthic response to TOC enrichment (Figure 9) that is consistent with the modified P - R curve by Hyland et al. (2005). An advantage of our model is that the impact of the freshness (degradation rate) of OC on modulating the benthic response is quantitatively distinguished.

The general validity of our model for a wide range of environmental conditions as typically found in coastal seas has larger implications for ecosystem modeling. Only very few complex dynamic models of the marine food web describe changes in infaunal biomass, but, so far, neglected both the vertical distribution of infauna activity as well as the two-way interaction with benthic TOC content and degradation (Baretta et al., 1995). This has been realized in our approach. Its more immediate usage may arise in biogeochemical studies where the transport of solid material within sediments is often represented in a rudimentary way. Our sensitivity analysis reveals site-specific changes in simulated TOC content from 10% to 50% at depth below 10 cm depending on the assumed vertical profile of bioturbation (Figure 6). These uncertainties clearly affect the estimated fluxes in oxygen, carbon, or mineral nutrients. The quantitative relevance of the vertical distribution in bioturbation intensity for major fluxes has already been shown by previous studies (e.g., Morse & Eldridge, 2007; Soetaert & Middelburg, 2009). The simplicity of our model formulations presented here may facilitate their implementation in biogeochemical or diagenesis models both in one and three

dimensions. In particular, the mechanistic linkage to varying OC inputs may enhance the accuracy of flux estimates by three-dimensional biogeochemistry models. On the other hand, a coupling with three-dimensional biogeochemistry models may help to better define some critical parameters such as L_1 and L_2 by associating them with oxygen and contamination levels and thus will improve the performance of our model. As the linkage emphasizes the role of food quality, we suggest a wider applicability of the model especially for oceanic sites where sharp spatial and/or temporal gradients of abundance, community composition, and activity of benthic animals exist (e.g., Pennington et al., 2006; Rosenberg, 2001).

5. Conclusions

Three major conclusions can be drawn from this study. First, a satisfactory agreement between field data from the North Sea and our simulation results sustains a mechanistic link between TOC and the community structure and biomass of macrobenthos in marine sediments, at least for nonseverely anoxic and nontoxic environments. The vertical distribution of biomass is shaped by both the quantity and quality (measured by the degradation rate) of OC, while the community structure is determined only by the quality of OC. Second, macrobenthos and TOC are mutually dependent on each other, as bioturbation affects the TOC distribution significantly. Bioturbation is a key process for all major biogeochemical fluxes at the sediment-water interface and is here, for the first time, described in terms of local food resource and infaunal microbial biomass. Bioturbation diffusivity may differ by 1 order of magnitude over different seasons owing to variations in the OC input according to our simulation result. Thus, the linkage to local macrobenthic characteristics will enhance physical soundness in models for benthic-pelagic coupling. Finally, our model results indicate that the community structure of macrobenthos in terms of biomass is dominated by deep-living feeders at low-to-intermediate food quality and by surface feeders at high food quality. In summary, our study emphasizes the need to integrate so far separated models of benthic ecology and biogeochemistry for a better and also quantitative understanding of processes at the sediment-water interface.

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References

- Baretta, J. W., Ebenhö, W., & Ruardij, P. (1995). The European regional seas ecosystem model (ERSEM), a complex marine ecosystem model. *Netherlands Journal of Sea Research*, *33*, 233–246. [https://doi.org/10.1016/0077-7579\(95\)90047-0](https://doi.org/10.1016/0077-7579(95)90047-0)
- Berg, P., Rysgaard, S., & Thamdrup, B. (2003). Dynamic modeling of early diagenesis and nutrient cycling. A case study in an arctic marine sediment. *American Journal of Science*, *303*, 905–955. <https://doi.org/10.2475/ajs.303.10.905>
- Berner, R. A. (1980). Early diagenesis: A theoretical approach. In N. J. Princeton (Ed.), *Princeton Series in Geochemistry* (pp. 241–256). Princeton, NJ: Princeton University Press.
- Blair, N. E., & Aller, R. C. (2012). The fate of terrestrial organic carbon in the marine environment. *Annual Review of Marine Science*, *4*, 401–423. <https://doi.org/10.1146/annurev-marine-120709-142717>
- Boudreau, B. (1997). *Diagenetic Models and their Implementation: Modelling Transport and Reactions in Aquatic Sediments* (pp. 414). Berlin: Springer.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1,771–1,789.
- Burdige, D. J. (2007). Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets? *Chemical Reviews*, *107*, 467–485. <https://doi.org/10.1021/cr050347q>
- Dauwe, B., Herman, P. M. J., & Heip, C. H. R. (1998). Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Marine Ecology Progress Series*, *173*, 67–83. <https://doi.org/10.3354/meps173067>
- Dhakar, S. P., & Burdige, D. J. (1996). A coupled, non-linear, steady state model for early diagenetic processes in pelagic sediments. *American Journal of Science*, *296*, 296–330. <https://doi.org/10.2475/ajs.296.3.296>
- Duplisa, D. E. (2000). Benthic organism biomass size-spectra in the Baltic Sea in relation to the sediment environment. *Limnology and Oceanography*, *45*, 558–568. <https://doi.org/10.4319/lo.2000.45.3.0558>
- Gooday, A. J., & Turley, C. M. (1990). Responses by benthic organisms to inputs of organic material to the ocean floor: A review. *Philosophical Transactions. Royal Society of London*, *331*, 119–138. <https://doi.org/10.1098/rsta.1990.0060>
- Grebmeier, J. M., McRoy, C. P., & Feder, H. M. (1988). Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas: I. Food supply source and benthic biomass. *Marine Ecology Progress Series*, *48*, 57–67. <https://doi.org/10.3354/meps048057>
- Hedges, J. I., & Keil, R. G. (1995). Sedimentary organic matter preservation: An assessment and speculative synthesis. *Marine Chemistry*, *49*, 81–115. [https://doi.org/10.1016/0304-4203\(95\)00008-F](https://doi.org/10.1016/0304-4203(95)00008-F)
- Heip, C., Basford, D., Craeymeersch, J. A., Dewarumez, J.-M., Dörjes, J., de Wilde, P., ... Soltwedel, T. (1992). Trends in biomass, density and diversity of North Sea macrofauna. *ICES Journal of Marine Science*, *49*, 13–22. <https://doi.org/10.1093/icesjms/49.1.13>
- Henrichs, S. M. (1992). Early diagenesis of organic matter in marine sediments: Progress and perplexity. *Marine Chemistry*, *39*, 119–149. [https://doi.org/10.1016/0304-4203\(92\)90098-U](https://doi.org/10.1016/0304-4203(92)90098-U)
- Herman, P. M. J., Middelburg, J. J., Van de Koppel, J., & Heip, C. H. R. (1999). The ecology of estuarine macrobenthos. *Advances in Ecological Research*, *29*, 195–240. [https://doi.org/10.1016/S0065-2504\(08\)60194-4](https://doi.org/10.1016/S0065-2504(08)60194-4)
- Hyland, J., Balthis, L., Karakassis, I., Magni, P., Petrov, A., Shine, J., ... Warwick, R. (2005). Organic carbon content of sediments as an indicator of stress in the marine benthos. *Marine Ecology Progress Series*, *295*, 91–103. <https://doi.org/10.3354/meps295091>
- Jørgensen, B. B. (1978). A comparison of methods for quantification of bacterial sulfate reduction in coastal marine sediments: 2. Calculation from mathematical models. *Geomicrobiology Journal*, *1*, 29–47. <https://doi.org/10.1080/01490457809377722>

- Jørgensen, B. B., & Parkes, R. J. (2010). Role of sulfate reduction and methane production by organic carbon degradation in eutrophic fjord sediments (Limfjorden, Denmark). *Limnology and Oceanography*, 55(3), 1,338–1,352. <https://doi.org/10.4319/lo.2010.55.3.1338>
- Jourabchi, P., Van Cappellen, P., & Regnier, P. (2005). Quantitative interpretation of pH distributions in aquatic sediments: A reaction-transport modeling approach. *American Journal of Science*, 305, 919–956. <https://doi.org/10.2475/ajs.305.9.919>
- Kamp, A., & Witte, U. (2005). Processing of ¹³C-labelled phytoplankton in a fine-grained sandy-shelf sediment (North Sea): relative importance of different macrofauna species. *Marine Ecology Progress Series*, 297, 61–70. <https://doi.org/10.3354/meps297061>
- Katsev, S., Rancourt, D. G., & Heureux, I. L. (2004). dSED: A database tool for modeling sediment early diagenesis. *Computational Geosciences*, 30, 959–967. <https://doi.org/10.1016/j.cageo.2004.06.005>
- Kelly-Gerreyn, B. A., Martin, A. P., Bett, B. J., Anderson, T. R., Kaariainen, J. I., Main, C. E., ... Yool, A. (2014). Benthic biomass size spectra in shelf and deep-sea sediments. *Biogeosciences*, 11, 6,401–6,416.
- Kristensen, E., Ahmed, S. I., & Devol, A. H. (1995). Aerobic and anaerobic decomposition of organic matter in marine sediment: Which is fastest? *Limnology and Oceanography*, 40, 1,430–1,437. <https://doi.org/10.4319/lo.1995.40.8.1430>
- Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. O., & Banta, G. T. (2012). What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, 446, 284–302. <https://doi.org/10.3354/meps09506>
- Kröncke, I. (2006). Structure and function of macrofaunal communities influenced by hydrodynamically controlled food availability in the Wadden Sea, the open North Sea, and the Deep-Sea. *Asynopsis. Senckenbergiana Maritima*, 36(2), 123–164. <https://doi.org/10.1007/BF03043725>
- Lee, A. J. (1980). North Sea: Physical oceanography. In F. T. Banner, M. B. Collins, & K. S. Massie (Eds.), *The North-West European Shelf Seas: The Sea Bed and the Sea in Motion. II. Physical and Chemical Oceanography, and Physical Resources* (pp. 467–493). Amsterdam: Elsevier.
- Levin, L. A., Ekau, W., Gooday, A. J., Jorissen, F., Middelburg, J. J., Naqvi, S. W. A., ... Zhang, J. (2009). Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences*, 6, 2063–2098. <https://doi.org/10.5194/bg-6-2063-2009>
- Lopez, G. R., & Levinton, J. S. (1987). Ecology of deposit-feeding animals in marine sediment. *The Quarterly Review of Biology*, 62, 235–260. <https://doi.org/10.1086/415511>
- Marcus, N. H., & Boero, F. (1998). Minireview: The importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnology and Oceanography*, 43(5), 763–768. <https://doi.org/10.4319/lo.1998.43.5.0763>
- Meysman, F. J. R., Middelburg, J. J., & Heip, C. H. R. (2006). Bioturbation: A fresh look at Darwin's last idea. *Trends in Ecology & Evolution*, 21, 688–695. <https://doi.org/10.1016/j.tree.2006.08.002>
- Middelburg, J. J., Vlug, T., & van der Nat, F. J. W. A. (1993). Organic matter mineralization in marine systems. *Global and Planetary Change*, 8, 47–58. [https://doi.org/10.1016/0921-8181\(93\)90062-5](https://doi.org/10.1016/0921-8181(93)90062-5)
- Morse, J. W., & Eldridge, P. M. (2007). A non-steady state diagenetic model for changes in sediment biogeochemistry in response to seasonally hypoxic/anoxic conditions in the “dead zone” of the Louisiana shelf. *Marine Chemistry*, 106(1–2), 239–255. <https://doi.org/10.1016/j.marchem.2006.02.003>
- Navarrete, S. A., Wieters, E. A., Broitman, B. R., & Castilla, J. C. (2005). Scales of benthic-pelagic coupling and the intensity of species interactions: From recruitment limitation to top-down control. *PNAS*, 102(50), 18,046–18,051. <https://doi.org/10.1073/pnas.0509119102>
- Nihoul, J. C. J. (1980). Residual circulation, long waves and mesoscale eddies in the North Sea. *Oceanologica Acta*, 3(3), 309–316.
- Ogawa, H., & Tanoue, E. (2003). Dissolved organic matter in oceanic waters. *Journal of Oceanography*, 59, 129–147. <https://doi.org/10.1023/A:1025528919771>
- Pearson, T. H., & Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology. Annual Review*, 16, 229–311.
- Pearson, T. H., & Rosenberg, R. (1987). Feast and famine: Structuring factors in marine benthic communities. In J. H. R. Gee, & P. S. Giller (Eds.), *The 27th Symposium of the British Ecological Society, Aberystwyth 1986* (pp. 373–395). Oxford: Blackwell Scientific Publications.
- Pennington, J. T., Mahoney, K. L., Kuwahar, V. S., Kolber, D. D., Calienes, R., & Chavez, F. P. (2006). Primary production in the eastern tropical Pacific: A review. *Progress in Oceanography*, 69(2–4), 285–317. <https://doi.org/10.1016/j.pocean.2006.03.012>
- Queirós, A. M., Birchenough, S. N. R., Bremner, J., Godbold, J. A., Parker, R. E., Romero-Ramirez, A., ... Widdicombe, S. (2013). A bioturbation classification of European marine infaunal invertebrates. *Ecology and Evolution*, 3(11), 3958–3985. <https://doi.org/10.1002/ece3.769>
- Reiss, H., & Kröncke, I. (2005). Seasonal variability of infaunal community structures in three areas of the North Sea under different environmental conditions. *Estuarine, Coastal and Shelf Science*, 65, 253–274. <https://doi.org/10.1016/j.ecss.2005.06.008>
- Rodil, I. F., Cividanes, S., Lastra, M., & Lopez, J. (2008). Seasonal variability in the vertical distribution of benthic macrofauna and sedimentary organic matter in an estuarine beach (NW Spain). *Estuaries and Coasts*, 31, 382–395. <https://doi.org/10.1007/s12237-007-9017-4>
- Rosenberg, R. (1995). Benthic marine fauna structured by hydrodynamic processes and food availability. *Netherlands Journal of Sea Research*, 34, 303–317. [https://doi.org/10.1016/0077-7579\(95\)90040-3](https://doi.org/10.1016/0077-7579(95)90040-3)
- Rosenberg, R. (2001). Marine benthic faunal successional stages and related sedimentary activity. *Scientia Marina*, 65, 107–119. <https://doi.org/10.3989/scimar.2001.65s2107>
- Schmidt-Nielsen, K. (1984). *Scaling—Why is Animal Size so Important?* Cambridge, UK: Cambridge University Press.
- Schwartzkopf, T. A. (1993). Model for prediction of organic carbon in possible source rocks. *Marine and Petroleum Geology*, 10, 478–492. [https://doi.org/10.1016/0264-8172\(93\)90049-X](https://doi.org/10.1016/0264-8172(93)90049-X)
- Soetaert, K., Herman, P. M. J., & Middelburg, J. J. (1996). A model of early diagenetic processes from the shelf to abyssal depths. *Geochimica et Cosmochimica Acta*, 60, 1019–1040. [https://doi.org/10.1016/0016-7037\(96\)00013-0](https://doi.org/10.1016/0016-7037(96)00013-0)
- Soetaert, K., & Middelburg, J. J. (2009). Modeling eutrophication and oligotrophication of shallow-water marine systems: The importance of sediments under stratified and well-mixed conditions. *Hydrobiologia*, 629, 239–254. <https://doi.org/10.1007/s10750-009-9777-x>
- Soetaert, K., Middelburg, J. J., Herman, P. M. J., & Buis, K. (2000). On the coupling of benthic and pelagic biogeochemical models. *Earth Science Reviews*, 51(1–4), 173–201. [https://doi.org/10.1016/S0012-8252\(00\)00004-0](https://doi.org/10.1016/S0012-8252(00)00004-0)
- Stanev, E., Dobrynin, M., Pleskachevsky, A., Grayek, S., & Günther, H. (2009). Bed shear stress in the southern North Sea as an important driver for suspended sediment dynamics. *Ocean Dynamics*, 59(2), 183–194. <https://doi.org/10.1007/s10236-008-0171-4>
- Sturdivant, S. K., Brush, M. J., & Diaz, R. J. (2013). Modeling the effect of hypoxia on macrobenthos production in the lower Rappahannock River, Chesapeake Bay, USA. *PLoS One*, 8(12), e84140. <https://doi.org/10.1371/journal.pone.0084140>
- Teal, L. R., Bulling, M. T., Parker, E. R., & Solan, M. (2008). Global patterns of bioturbation intensity and mixed depth of marine soft sediments. *Aquatic Biology*, 2, 207–218. <https://doi.org/10.3354/ab00052>
- Venturini, N., Pires-Vanin, A. M. S., Salhi, M., Bessonart, M., & Muniz, P. (2011). Polychaete response to fresh food supply at organically enriched coastal sites: Repercussion on bioturbation potential and trophic structure. *Journal of Marine Systems*, 88(4), 526–541. <https://doi.org/10.1016/j.jmarsys.2011.07.002>

- Ward, B. A., Friedrichs, M. A. M., Anderson, T. R., & Oschlies, A. (2010). Parameter optimisation techniques and the problem of underdetermination in marine bio-geochemical models. *Journal of Marine Systems*, *81*, 34–43.
- Westrich, J. T., & Bemer, R. A. (1984). The role of sedimentary organic matter in sulfate reduction: The G-model testes. *Limnology and Oceanography*, *29*, 236–249. <https://doi.org/10.4319/lo.1984.29.2.0236>
- Whearcroft, R. A., Jumars, P. A., Smith, C. R., & Nowell, A. R. M. (1990). A mechanistic view of particulate biodiffusion coefficient: Step lengths, rest periods and transport directions. *Journal of Marine Research*, *48*, 177–207.
- Wieking, G., & Kröncke, I. (2003). Macrofauna communities of the Dogger Bank (central North Sea) in the late 1990s: Spatial distribution, species composition and trophic structure. *Helgoland Marine Research*, *57*, 34–46. <https://doi.org/10.1007/s10152-002-0130-2>
- Wieking, G., & Kröncke, I. (2005). Is benthic trophic structure affected by food quality? The Dogger Bank example. *Marine Biology*, *146*, 387–400. <https://doi.org/10.1007/s00227-004-1443-2>
- Wijsman, J. W. M., Herman, P. M. J., Middelburg, J. J., & Soetaert, K. (2002). A model for early diagenetic processes in sediments of the continental shelf of the Black Sea. *Estuarine, Coastal and Shelf Science*, *54*, 403–421. <https://doi.org/10.1006/ecss.2000.0655>